Landscape Evaluation of Grizzly Bear Habitat in Western Montana

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Abstract: *We present a method for evaluating the cumulative effects of human activity on grizzly bear (*Ursus arctos*) habitat in the Northern Continental Divide Ecosystem of western Montana. Using logistic regression, we modeled the relative probabilities of female grizzly bear resource selection from telemetry data, TM satellite imagery (greenness), elevation, human activity points, roads, and trails. During spring, adult female grizzly bears were positively associated with low- and mid-elevation habitats. Logistic regression coefficients were negative for all road and human activity variables. Summer and fall coefficients were also negative for road, human activity, and trail variables. During summer and fall, females were positively associated with mid to high elevations. Coefficients were positive for greenness during all seasons. Extrapolations of seasonal potential and realized habitat models were made to other areas on the western side of the region where no telemetry data existed. During spring, much of the Bob Marshall Wilderness exhibited a relatively low probability of use by female grizzly bears, but the converse was observed during summer and fall. The mapping and extrapolation process highlighted areas where habitat restoration would have the greatest benefit. These areas were typically low-elevation spring habitats with high road densities and private lands where urbanization occurred. We recommend that habitat management agencies implement reductions in road densities in seasonal habitat and implement methods to maintain habitat function on private lands.*

Evaluación de Paisaje del Hábitat del Oso Grizzly en el Oeste de Montana

Resumen: *Presentamos un método para la evaluación de efectos acumulativos de actividades humanas en el hábtat del oso grizzly (*Ursus arctos*) en el Ecosistema Norte de Montana Occidental. Modelamos las probabilidades de selección de recursos de hembras del oso grizzly utilizando regresión logística con datos de telemetría, imagen de satélite TM (intensidad del verde), elevación, puntos de actividad humana, carreteras y veredas. Durante la primavera, las hembras adultas estuvieron postivamente asociadas con hábitats de elevación baja y media. Los coeficientes de regresión logística fueron negativos para las carreteras y las variables de actividad humana. En verano y Otoño los coeficientes fueron también negativos para carreteras, actividades humanas y veredas. Durante el verano y el otoño, las hembras estuvieron positivamente asociadas con elevacones medias y altas. Los coeficientes fueron positivos para la intensidad del verde en todas las estaciones. Extrapolaciones de modelos de potencial estacional y hábitat realizado fueron construídos para otras áreas de la región oeste, donde no se han generado datos de telemetría. Durante la primavera, una gran porción de la región de vida silvestre Bob Marshal exhibió probabilidades de uso relativamente bajas, pero se observó lo contrario durante el verano y el otoño. El mapeo y la extrapolación resaltó áreas donde la restauración del hábitat podría proveer los mayores beneficios. Estas áreas son típicamente hábitats de arroyos con baja elevación, con alta densidad de carreteras y tierras privadas donde ha ocurrido urbanización. Recomendamos que las agencias de manejo implementen reducciones en la densidad de carreteras en hábitats estacionales e implementen métodos para mantener la función del hábitat en tierras privadas.*

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Introduction

Wildlife managers have long sought to understand how human activities affect the suitability of habitat for various wildlife species. The literature abounds with assessments of the effects of land conversion, land-use practices, urbanization, and pollution on wildlife demography, energetics, nutrition, and survival (Berry 1986). Most studies emphasize animal response to a single variable. Early efforts to incorporate multiple factors included "habitat suitability models" that were generally a series of univariate models combined into a single model.

Significant improvements in habitat suitability models followed advances in spatial statistics, habitat selection statistics, satellite imagery, and computer mapping (Stormer & Johnson 1986). These advances improved evaluations of the effects of human occupation on wildlife at landscape and ecosystem scales (Craighead et al. 1982).

Models evaluating the effects of multiple human activities on grizzly bear habitat—"cumulative effects models" (CEM)—were first conceptualized in the early 1980s (Christensen 1986). Early CEM efforts relied heavily on the "delphi method" in which group consensus was used to quantify relationships between human activities and grizzly bears. Recent studies of grizzly bear demography (Mace et al. 1994; Mace & Waller 1998) and habitat selection (Mace et al. 1996; Waller & Mace 1998) have formed the foundation for a more comprehensive, empirically based CEM.

We present a landscape-scale evaluation of grizzly bear habitat for three seasons by modeling potential and realized habitat effectiveness using resource selection functions (Manly et al. 1993). We define *potential habitat effectiveness* as the relative probability of grizzly bears using landscape features in the absence of human activity and *realized habitat effectiveness* as the relative probability of grizzly bears using landscape features in the presence of human activities. Further, we present an analytical method that will enable managers to more easily interpret CEM outputs and that will direct managers to those areas with the greatest potential for restoration or protection efforts. We also demonstrate the usefulness of this technique in a broader landscape perspective by extrapolating model parameters to other portions of the western Northern Continental Divide Ecosystem (NCDE).

Study Areas

The 24,262-km^2 NCDE, one of six designated grizzly bear recovery areas (U.S. Fish and Wildlife Service 1993), is located in the Rocky Mountain Cordillera of western Montana. The Continental Divide bisects the ecosystem. Portions west of the Divide are characterized by a Pacific Maritime climate (cool, wet summers and warm, wet winters), mesic habitats, and lower average elevations. Portions east of the Divide have a continental climate (hot, dry summers and cold, dry winters), with more xeric habitats (Pfister et al. 1977) and higher average elevations.

We conducted the telemetry study in 1457 km^2 of the Swan Mountain Range in the western NCDE (Fig. 1). The area is bounded on the north by U.S. Highway 2 and on the south by the Bob Marshall Wilderness. Hungry Horse Reservoir and the Flathead River and Swan River valleys form the east and west boundaries, respectively. The study area is of rugged mountain topography, and elevations vary from 914 m to 2736 m. Although heavily forested, the higher elevations contain mixtures of natural burns, avalanche chutes, rock lands, and grass lands. Fifteen percent of the telemetry study area (TSA) has some history of timber harvest (Waller 1992).

The TSA is composed of private, corporate, state, and federal land ownerships. State, corporate, and federal lands are managed primarily for timber harvest, recreation, and wildlife values. Private lands (9% of area) are in the Flathead Valley east of the city of Kalispell and in the Swan River Valley. Most private lands are developed for permanent homes, farms, and service facilities. Beginning in the late 1940s, a network of roads was established within the study area primarily to access timber and to construct Hungry Horse Dam (Mace et al. 1996).

The extrapolation area (EA) included 4690-km^2 portions of the western side of the NCDE judged to have similar climate and vegetation. The extrapolation area was used to some extent between 1987 and 1995 by radio-collared male and female grizzly bears (Mace & Waller 1998). In addition to private, state, and corporate lands, the EA included portions of the Mission Mountain and the Bob Marshall and Great Bear wilderness areas. Private lands within the EA occurred primarily in the Swan Valley and between Glacier National Park and the Great Bear Wilderness. Together, the TSA and EA constituted about 25% of the NCDE.

Methods

Capture and Telemetry

Beginning in 1987, adult ($\geq$5 years old) and subadult grizzly bears were captured and radio-collared in the TSA (Mace et al. 1994). Radio-collared grizzly bears were diurnally located 1–3 times each week from fixed-wing aircraft. Our radio-collared bears tended not to be active at night (Mace & Waller 1997). We used telemetry data collected from 1987 through 1996 from eight adult females. Telemetry sample size was similar for each of the eight individuals (within two standard deviations of the group mean each season). Relocations were grouped into seasons based on major changes in the primary food plants consumed by grizzly bears (Craighead et al. 1982;

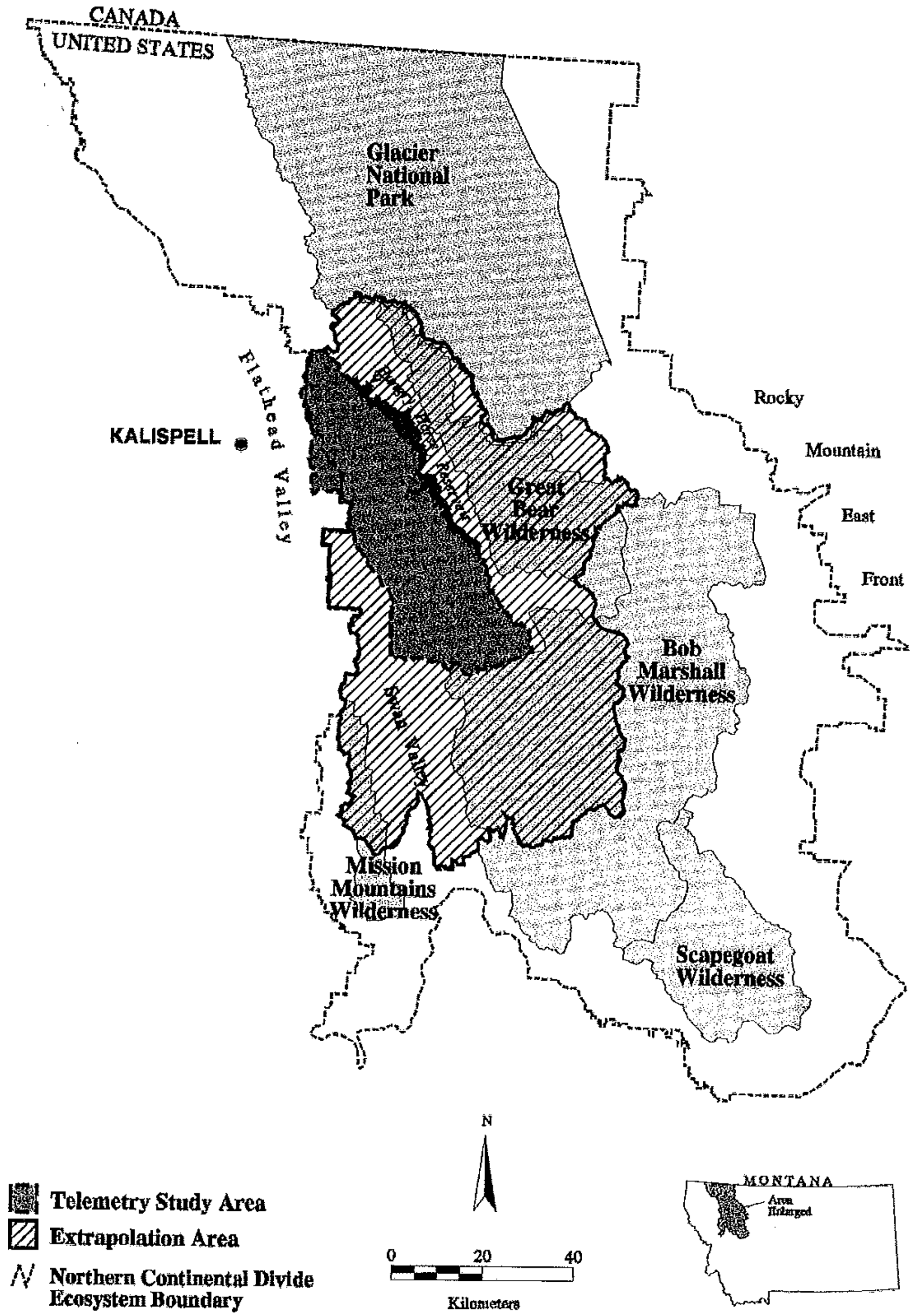

Figure 1. Location of the telemetry study area in the Swan Mountains, where seasonal resource selection functions were developed. These functions were then extrapolated to a larger portion of the western Northern Continental Divide Ecosystem.

Mace & Jonkel 1983). Spring was defined as that period after each bear left the vicinity of its winter den until 15 July. Summer was defined as 16 July to 15 September. Fall was 16 September to the time when each grizzly bear denned. Telemetry sample sizes were 517 locations during spring, 412 during summer, and 244 during fall. A Universal Transverse Mercator coordinate was assigned to each relocation. Relocations were then converted to computer geographic information system (GIS) maps with the GIS software EPPL7 (Minnesota State Planning Agency, St. Paul). Maps were in a raster format with a pixel size of 30 × 30 m.

Map Layers

ROADS AND TRAILS

All roads and trails in the study areas were obtained in digital form from the U.S. Forest Service and verified in the field. Each road was categorized as legally open or closed to public vehicular travel each season. Old roads reclaimed by vegetation were not mapped.

We used 10 magnetic counters to quantify levels of vehicle traffic on a sample of roads from 1990 to 1992 (Mace et al. 1996). Using these traffic volume data and extrapolations based on knowledge of the study area, we categorized each road segment into three levels of vehicular traffic for each season: low, <1 vehicle/day; moderate, 1–10 vehicles/day; and high, >10 vehicles/day. The road network of each traffic volume class was then converted to a road density map with a 1-km^2 moving-window GIS routine. The EPPL7 moving-window routine calculated road kilometers per square kilometer for each pixel in the study area (Mace et al. 1996). Road density maps were categorized as 0, 0 km road/km^2 (unroaded); 1, >0 and ≤0.5 km road/km^2; 2, >0.5 and ≤1.0 km road/km^2; 3, >1.0 and ≤1.5 km road/km^2; 4, >1.5 and ≤2.0 km road/km^2; and 5, >2.0 km road/km^2.

We did not have detailed knowledge of seasonal human use levels on the trail system in the study areas. Therefore, to match the mapping scale used for roads, we buffered the trail system by 0.5 km (Kasworm & Manley 1990; Mace & Waller 1996; Mace et al. 1996). Only those trails maintained by the U.S. Forest Service were used.

HUMAN POINT DISTURBANCE

All known points of human activity were digitized as potential disturbance sources. Point disturbances varied from periodically used camping areas to permanently occupied residences. We subjectively grouped the points as having low or high impacts on grizzly bear distribution based on the following criteria: amount of human activity, probable activities that humans would engage in at each point type, presence of attractants (e.g., food, garbage, livestock), noise levels, and duration of activity. Point disturbance maps were then buffered by 0.5 km to match road and trail layers.

PSEUDO-HABITAT AND ELEVATION

A classified, validated habitat map for the NCDE did not exist; therefore, we used a 28 August 1988 LANDSAT Thematic Mapper (TM) satellite image to develop a pseudo-habitat map. Following atmospheric corrections (Jensen 1986), the image was transformed into brightness, wetness, and greenness bands by the tasseled cap transformation (Crist & Cicone 1984; Manley et al. 1992). Increasing values of greenness related to increased amounts of deciduous, green vegetation (e.g., leaf area index). We selected the greenness band, categorized into 10 classes of increasing greenness, as an indicator of grizzly bear habitat. Earlier univariate tests revealed strong selection for areas of high greenness by grizzly bears.

We classified a digital elevation map into three zones based on dominant conifer species (Montana Fish, Wildlife and Parks, unpublished data). The low temperate zone extended from 914 m to the lower limit of subalpine fir (*Abies lasiocarpa*) at 1494 m. The temperate zone extended to the upper limit of Douglas fir (*Pseudotsuga menziesii*) and western larch (*Larix occidentalis*) at 1981 m. Elevations above 1981 m were classified as the subalpine zone. In the logistic models, we used the subalpine zone as the standard against which the low temperate and temperate zones varied (Hosmer & Lemeshow 1989).

Model Building Methods

We used logistic regression, seasonal telemetry locations, and an equal number of random coordinates to model the probability of occurrence of adult female grizzly bears as a function of map variables in the TSA (Pereira & Itami 1991; Manly et al. 1993; Mace et al. 1996). For each season, we calculated resource selection functions (RSF) for used (telemetry) and available (random) resources using equation 8.7 from Manly et al. (1993:127):

$$w(x) = \exp(\beta_1 x_1 + \ldots + \beta_p x_p), \tag{1}$$

where $w(x)$ was the RSF and $\beta_1 x_1 + \ldots + \beta_p x_p$ represented the available resource units. The RSF values represented the relative probability of an adult female grizzly bear using each unique variable combination. Our methods followed "design II," in which use of resource units by individual animals was evaluated relative to the availability of those units in the entire study area (Manly et al. 1993:6).

In previous publications, we incorporated a 150-m aerial telemetry error into all map layers using a moving-window routine. Within this error polygon, map features were generalized by ascribing the dominant map feature to each error polygon (Mace & Waller 1996; Mace et al. 1996; Waller & Mace 1998). Here, we opted not to incorporate telemetry error because elevation, road, trail, and point features were generalized by a 0.50-km buffer. Telemetry error was not incorporated into the pseudo-habitat map layer because preliminary tests showed no difference in the distribution of telemetry points between buffered and nonbuffered maps (Mann-Whitney $p \geq 0.48$).

Logistic regression modeling may include univariate tests of variables and the derivation of a final model containing only significant variables (Hosmer & Lemeshow 1989). We were interested in the cumulative effect of all the chosen variables on habitat selection of females and therefore did not omit variables that were either univariately insignificant ($p \geq 0.05$) or that were insignificant in logistic models. Although inclusion of insignificant variables reduced the efficiency of the model, parameter estimates remained unbiased (Menard 1995). The logistic regression coefficients represented the contribution of each variable to explaining grizzly bear resource selection relative to random availability. The association and power of each variable was ascertained by each coefficient's sign (negative or positive) and strength (p value). Significant negative coefficients implied avoidance, whereas significant positive coefficients suggested attraction. Seasonal models that significantly reduced the -2log-likelihood ratios ($p \leq 0.05$) from the null models were considered suitably fitted (Hosmer & Lemeshow 1989; Menard 1995).

The RSF values were scaled from 0% to 100% by dividing each unscaled RSF value by the largest unscaled RSF value. The scaled values from the model were then used to create two GIS maps. The "potential" map represented the relative probability of occurrence of adult female grizzly bears in the absence of human activity. To develop the potential map, all coefficients for human activities, roads, and trails in the logistic model were replaced with zero. The "realized" map included the coefficients for human activities, roads, and trails. The difference in RSF values between the two maps was considered the reduction in habitat potential due to human development.

The pooled sample of eight adult females in the TSA was used to create the coefficients. We derived 95% confidence intervals for each coefficient in each season by creating a separate model for each $n - 1$ sample of individuals (jackknifing). This process allowed assessment of model stability and resource selection variability among individual bears. The significance of each coefficient was determined by its p value, calculated by dividing the coefficient by its asymptotic standard error (computed by finite differencing; Statistica 1995). Squaring the resulting quotient produces the Wald statistic, which follows a chi-square distribution.

We used standardized residuals (Menard 1995) to examine the distribution of errors and to detect cases where the model fit poorly. To establish the model's substantive significance, we calculated coefficients of determination (R^2) for each seasonal model by regressing use against predicted values (Menard 1995). Pearson 2×2 contingency tables were developed to measure classification accuracy using a predicted value of 50% probability as a decision point (Statistica 1995).

We developed potential and realized habitat effectiveness maps for each season for the EA by applying TSA coefficients. We used mean subunit RSF values to compare habitat potential and realized habitat effectiveness across the EA. Declines in habitat potential could be calculated as potential minus realized RSF values. But because declines in areas of high potential have a greater impact on bears than similar declines in areas of low potential, we used a simple weighting algorithm to calculate an adjusted percent change:

$$\text{adjusted percent change} = \frac{(\text{potential RSF} - \text{realized RSF}) \times \text{potential RSF}}{100}. \quad (2)$$

This process ranked declines in areas of high potential higher than similar declines in areas of low potential.

Bear management subunits are management areas in the NCDE used for grizzly bear population and habitat management. They were drawn by group consensus and typically encompass major drainages and portions of intervening ridges. Subunits averaged 128 km^2 and ranged from 83 km^2 to 187 km^2.

The TSA contained 12 subunits, and the EA contained 36 subunits. Average subunit potential and realized values were combined into various management units to compare the TSA to the EA, designated wilderness to nonwilderness, and the Bob Marshall Wilderness to the Great Bear Wilderness. The Mission Mountains Wilderness made up only small portions of three subunits, comprised only 2% of the total EA, and was therefore treated as nonwilderness. The Bob Marshall and Great Bear wilderness areas comprised 17 complete subunits and a much larger portion of the EA (24% and 13%, respectively). We used Kruskal-Wallis nonparametric analysis of variance to test comparisons between management units. Significance was accepted at $\alpha = 0.05$. The Swan Valley was not statistically compared to other units because it overlaps with other nonwilderness subunits and is clearly different from wilderness management units.

The sample of female grizzly bears used to build seasonal coefficients was those bears that survived long enough for us to gather telemetry data. Thus the model is biased toward those behaviors that contribute to longevity. Most of the grizzly bears that occupied the valley bottoms exclusively were killed during Anglo-American settlement. Selection pressure continued to operate against bears showing preference for low-elevation habitats during this study.

Results

Telemetry Study

The spring logistic model was significant ($-2LL = 1250.8$, $\chi^2 = 182.6$, df = 8, $p = 0.000$, $r^2 = 0.16$), and all variables except low-impact human activities made significant contributions. Errors were normally distributed, with mean = -0.005 and SD = 1.003. The model correctly classified 72% of used sites and 57% of random sites.

Our sample of adult female grizzly bears was most strongly associated with areas of high greenness in the low temperate zone. They were significantly and negatively associated with low, moderate, and high-use road densities (Fig. 2) and presence of high-impact human activity points (Table 1). Adult females were least affected by the presence of low-impact human activity points (Table 1).

The summer logistic model was significant ($-2LL = 965.4$, $\chi^2 = 176.9$, df = 9, $p = 0.000$, $r^2 = 0.19$), and significant variables were greenness and road density. Errors were normally distributed, with mean = 0.000 and SD = 0.993. The model correctly classified 76% of used sites and 60% of random sites.

During summer, as in spring, sample bears were strongly associated with high greenness. Elevation coefficients were negative for the low temperate zone and positive for the temperate relative to the subalpine zone, but they were not significant. Coefficients were negative for all human variables during summer, but only road-density variables were significant (Table 2).

The fall logistic model was significant ($-2LL = 576.1$, $\chi^2 = 100.4$, df = 8, $p = 0.000$, $r^2 = 0.19$) and correctly classified 77% of use sites and 58% of random sites. Model instability was observed, however, due to the absence of bear use in areas with high-impact human activities and very limited bear use in high-road density areas. High-impact use areas were omitted from the model, and areas on the maps where they occurred were assigned an RSF value of zero. Only one female used areas of high road density, resulting in a wide confidence interval for this variable (Table 3). Had she not been detected in high-road-density areas, this variable would also have been omitted from the model and coded as zero RSF.

Significant fall variables were greenness, elevation zone, and high-use road density. Moderate-use road density approached significance at $p = 0.07$ (Table 3). Our sample of females significantly avoided the low temperate elevation zone during this season.

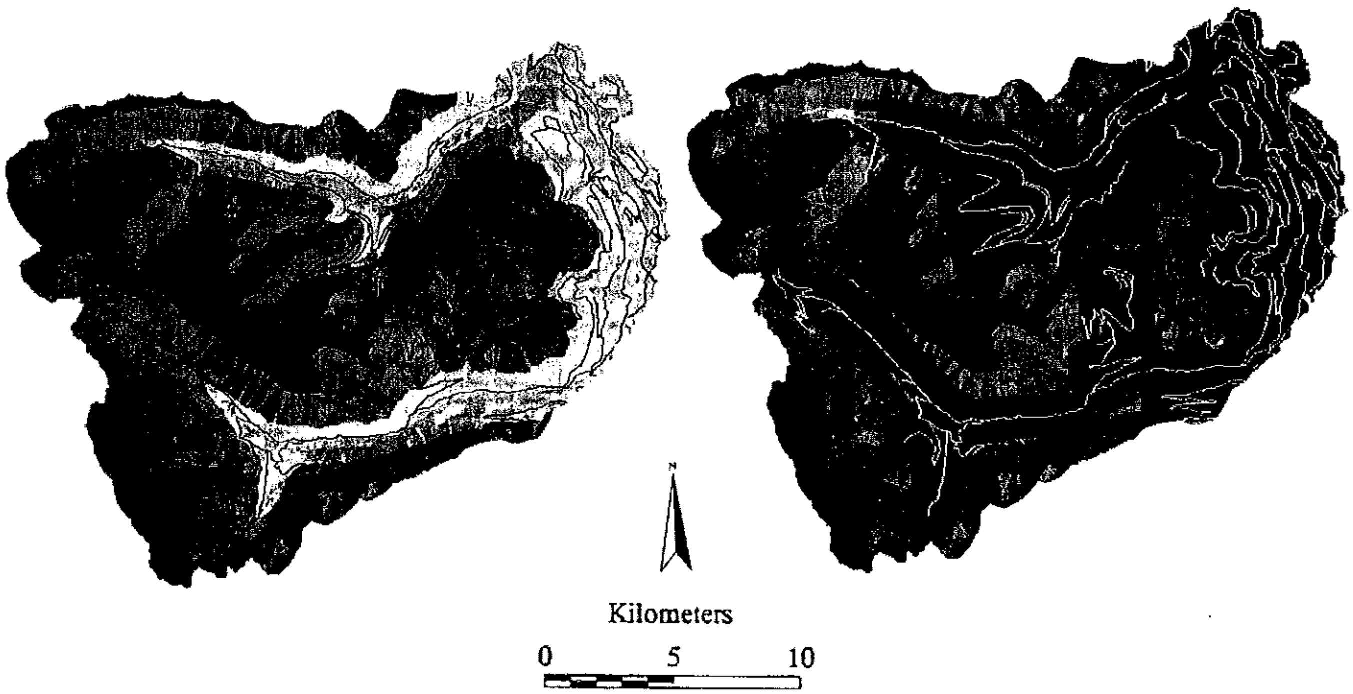

Figure 2. Maps of spring habitat, potential (left) and realized (right), of a 141-km² subunit in the telemetry study area. Each 30 × 30 m map pixel represents the relative probability of use by female grizzly bears; lighter areas represented higher resource selection function values. Average habitat potential in this subunit was reduced by high densities of forest roads, as shown.

Table 1. Mean spring logistic regression model coefficients, ±95% confidence intervals, range, standard error (SE), and significance levels from eight adult female grizzly bears, Swan Mountains, Montana.

	Coefficients							
Variable	*Mean*	*−95%*	*+95%*	*Minimum*	*Maximum*	*SE*	t	p
Constant	−0.8604	−0.9870	−0.7432	−0.9749	−0.5878	0.2837	−3.0329	0.0024
Greenness	0.1026	0.0784	0.1284	0.0660	0.1539	0.0320	3.2040	0.0014
Low-temperate zone	1.4095	1.2275	1.5866	0.9954	1.7140	0.2842	4.9586	0.0001
Temperate zone	0.8224	0.6874	0.9510	0.5524	0.9860	0.2316	3.5510	0.0004
Low-use road density	−0.5019	−0.5654	−0.4473	−0.6636	−0.4356	0.0614	−8.1705	0.0000
Moderate-use road density	−0.5462	−0.6412	−0.4650	−0.7401	−0.3986	0.1104	−4.9473	0.0001
High-use road density	−0.5065	−0.5751	−0.4510	−0.6365	−0.4254	0.1352	−3.7452	0.0002
Low-impact activity points	−0.0703	−0.1871	0.0409	−0.2869	0.0569	0.2562	−0.2743	0.7839
High-impact activity points	−1.5706	−1.2256	−0.9057	−1.6752	−0.9838	0.6007	−2.3180	0.0207

Spring habitat potential for subunits averaged 46% and ranged from 34% to 59%, whereas realized values averaged 24% and ranged from 19% to 28% (Table 4). Reductions (percent adjusted change) from spring habitat potential averaged 14% and ranged from 6% to 21%. Across all levels of greenness, the greatest average reduction from potential was due to high-impact human activities in low-temperate and temperate elevation zones, followed by moderate-use roads in low temperate and temperate elevation zones (Fig. 3). Low-impact activities had little effect during spring.

Summer habitat potential averaged 30% and ranged from 23% to 36%, whereas summer realized values averaged 19% and ranged from 13% to 29% (Table 4). Percent adjusted change from summer habitat potential averaged 4% and ranged from 3% to 6%. Across all levels of greenness, the greatest mean reduction from habitat potential was due to increasing high- and moderate-use road densities in low-temperate and temperate elevation zones. Trails and low-impact human activities had little effect (Fig. 3).

Fall habitat potential averaged 31% and ranged from 23% to 39%, and fall realized values averaged 22% and ranged from 13% to 33% (Table 4). Percent adjusted change from fall habitat potential averaged 3% and ranged from 2% to 5%. Across all levels of greenness, the greatest mean reductions from potential were due to high-impact human activities and increasing densities of high-use roads at low-temperate and temperate elevation zones (Fig. 3). As in spring and summer, trails and low-impact human activities had little effect.

Extrapolation Study

The application of TSA coefficients to the EA ensured that the same factors controlled RSF levels in the EA. Thus, the areas having the greatest potential were those similar to areas of high potential within the TSA. Potential was reduced by increasing road densities and high-impact human activity points.

Mean subunit potential was significantly greater in the TSA than the EA during spring ($H = 5.2$, df $= 1$, $p = 0.02$), but not during summer or fall. Mean subunit realized values were equal during all seasons, but the percent adjusted change was significantly greater in the TSA during all seasons ($H \geq 5.0$, df $= 1, p < 0.02$).

The average potential RSF value of nonwilderness subunits was significantly greater than that of wilderness

Table 2. Mean summer logistic regression model coefficients, ±95% confidence intervals, range, standard error (SE), and significance levels from eight adult female grizzly bears, Swan Mountains, Montana.

	Coefficients							
Variable	*Mean*	*−95%*	*+95%*	*Minimum*	*Maximum*	*SE*	t	p
Constant	−1.1371	−1.3375	−0.9448	−1.5301	−0.8522	0.3300	−3.4461	0.0006
Greenness	0.2351	0.2175	0.2552	0.2056	0.2751	0.0405	5.7970	0.0000
Low-temperate zone	−0.3569	−0.6062	−0.1308	−0.8587	0.1376	0.3027	−1.1790	0.2388
Temperate zone	0.2167	0.0711	0.3536	−0.0444	0.5436	0.2285	0.9483	0.3433
Trail buffer	−0.2620	−0.3652	−0.1827	−0.5269	−0.1821	0.1863	−1.4064	0.1601
Low-use road density	−0.2790	−0.3213	−0.2375	−0.3539	−0.2008	0.0993	−2.8100	0.0051
Moderate-use road density	−0.5912	−0.7637	−0.4643	−1.0022	−0.4150	0.1303	−4.5359	0.0001
High-use road density	−1.0372	−1.2428	−0.8943	−1.4742	−0.8246	0.3545	−2.9255	0.0036
Low-impact activity points	−0.1114	−0.2185	0.0082	−0.2925	0.0787	0.3105	−0.3586	0.7200
High-impact activity points	−1.1627	−1.4568	−0.8666	−1.7187	−0.6093	0.7863	−1.4788	0.1397

Table 3. Mean fall logistic regression model coefficients, ±95% confidence intervals, range, standard error (SE), and significance levels from eight adult female grizzly bears, Swan Mountains, Montana.

Variable	Coefficients					SE	t	p
	Mean	−95%	+95%	Minimum	Maximum			
Constant	−0.7181	−0.9848	−0.4652	−1.1746	−0.2974	0.3569	−2.0119	0.0449
Greenness	0.1989	0.1739	0.2272	0.1660	0.2501	0.0499	3.9840	0.0001
Low-temperate zone	−1.0481	−1.2659	−0.8471	−1.4066	−0.6511	0.3146	−3.3319	0.0010
Temperate zone	0.0001	−0.1498	0.1442	−0.3128	0.1816	0.0202	0.0070	0.9944
Trail buffer	−0.3500	−0.4423	−0.2711	−0.4828	−0.1558	0.2410	−1.4520	0.1473
Low-use road density	−0.1637	−0.2234	−0.1046	−0.2509	−0.0661	0.1188	−1.3774	0.1691
Moderate-use road density	−0.2862	−0.3607	−0.2141	−0.4106	−0.1509	0.1565	−1.8286	0.0682
High-use road density	−1.3110	−11.676	2.9960	−26.057	−1.0996	0.5881	−2.2294	0.0263
Low-impact activity points	−0.1994	−0.3543	−0.0496	−0.5187	0.0136	0.3920	−0.5086	0.6113

subunits during spring ($H = 24.0$, df $= 1, p = 0.00$), was the same during the summer, and was significantly lower during fall ($H = 5.0$, df $= 1, p = 0.03$). The average realized RSF value of nonwilderness subunits was significantly lower than that of wilderness subunits ($H \geq 12.2$, df $= 1, p < 0.01$) during all seasons (Table 4). Not surprisingly, reductions from potential in nonwilderness were significantly greater than in wilderness each season ($H \geq 7.8$, df $= 1, p < 0.00$).

The Great Bear Wilderness had significantly higher potential and realized RSF values than the Bob Marshall Wilderness during all seasons ($H \geq 4.4$, df $= 1, p \leq 0.03$; Table 4). Average reduction from potential in the Great Bear Wilderness was significantly greater ($H \geq 7.9$, df $= 1, p < 0.01$) than in the Bob Marshall Wilderness during summer and fall only.

Discussion

Our methodology modeled the cumulative impacts of human activity on grizzly bear habitat. During spring, female grizzly bears used low-elevation habitats, where winter snow melted first and succulent vegetation favored by bears appeared. These lower-elevation habitats also contained most of the human activities and roads, so reductions from potential were highest here during spring.

Females generally shifted to mid-elevations during summer, but use of other elevation zones continued, so coefficients for elevation during summer were insignificant. No strong avoidance of high-impact human activity points was noted during summer because of their absence from the mid-elevation zones used during summer.

During fall, female grizzly bears used mid- and high-elevation habitats and avoided low-elevation habitats. High densities of high-volume roads were strongly avoided, and no bears were observed near high-impact human activity points. These results suggest that there is value in road closures aimed at minimizing traffic on roads within important seasonal habitats, especially in low-elevation habitats during spring. Avoidance of habitats adjacent to roads and the negative impacts of high road densities and traffic volumes have been documented elsewhere for grizzly bears (Mattson et al. 1987; McLellan & Shackleton 1988; Kasworm & Manley 1990; Mace et al. 1996). Avoidance of low-impact human activ-

Table 4. Average seasonal mean subunit resource selection function (RSF)[a] values, mean percent adjusted change, and ranges (in parentheses) by research and management units, western Northern Continental Divide Ecosystem, Montana.

Management unit	Spring			Summer			Fall		
	Potential	Realized	Adjusted change	Potential	Realized	Adjusted change	Potential	Realized	Adjusted change
Telemetry area (TSA)	46 (34–59)	24 (19–28)	14 (6–21)	30 (23–36)	19 (13–29)	4 (3–6)	31 (23–39)	22 (13–33)	3 (2–5)
Extrapolation area (EA)	39 (22–56)	26 (10–42)	8 (0–26)	27 (18–39)	20 (5–32)	2 (0.5–6)	30 (14–41)	24 (5–37)	2 (1–5)
Wilderness[b]	31 (22–47)	30 (21–42)	1 (0–4)	27 (20–36)	24 (18–34)	1 (0.5–3)	33 (26–42)	29 (22–37)	2 (1–4)
Nonwilderness[c]	46 (29–59)	22 (10–36)	14 (4–26)	28 (18–39)	17 (5–32)	3 (1–6)	28 (14–41)	20 (5–34)	3 (1–5)
Bob Marshall[b]	27 (22–33)	27 (21–32)	0 (0–0)	24 (20–30)	22 (18–27)	1 (0.5–1)	31 (26–39)	27 (22–36)	1 (1–2)
Great Bear[b]	38 (30–47)	36 (30–42)	1 (0–4)	33 (27–38)	29 (24–34)	2 (1–3)	38 (32–42)	32 (27–37)	2 (1–4)
Swan Valley[d]	47 (40–54)	18 (10–28)	18 (11–23)	25 (20–31)	14 (6–19)	3 (1–6)	25 (20–30)	16 (8–23)	3 (1–5)

[a] *RSF values represent the relative probability of an adult female grizzly bear using each unique variable combination.*
[b] *Includes portions of the extrapolation area (EA).*
[c] *Includes portions of the telemetry study area (TSA).*
[d] *Includes portions of the EA and TSA.*

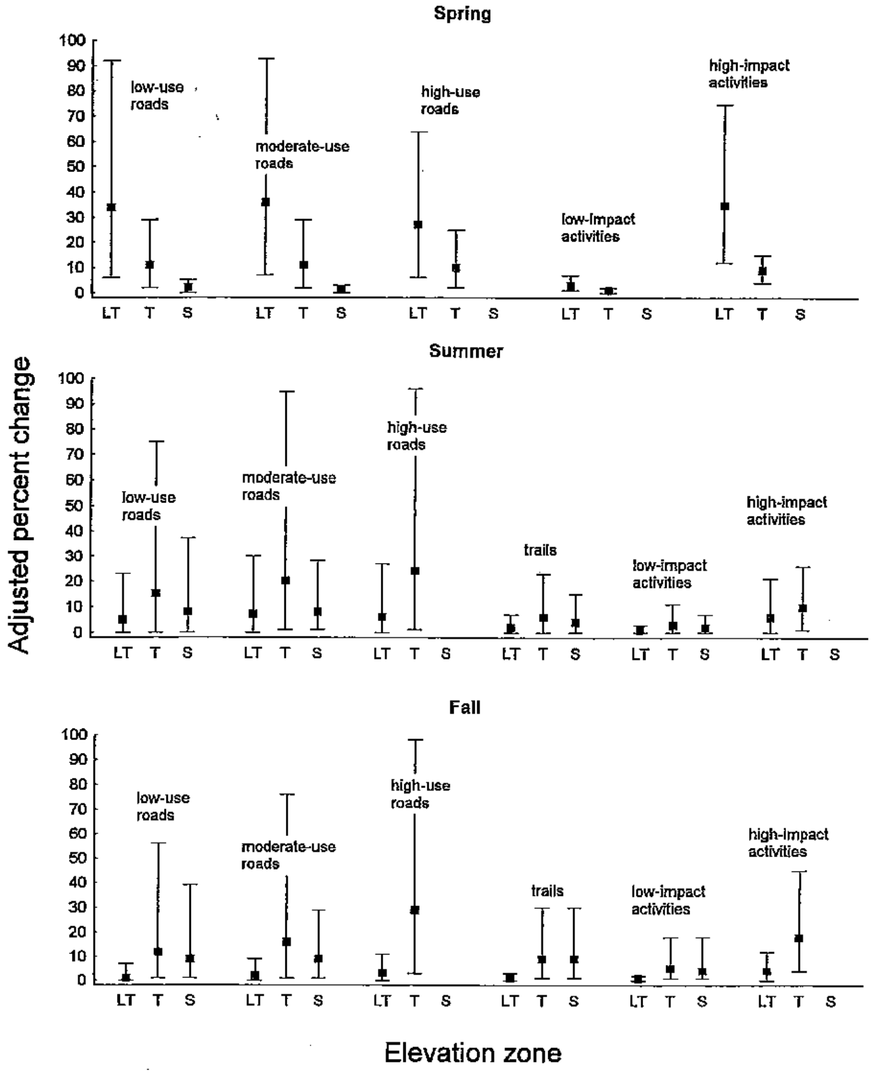

Figure 3. Adjusted percent change (mean and range) from habitat potential to realized habitat effectiveness for each season within the telemetry study due to roads, trails, and low- and high-use human point activities. Adjusted percent change values are provided for the low-temperate (LT), temperate (T), and subalpine (S) elevation zones. Percentages represent reduction from potential when all other human activity variables are absent and across all levels of greenness (Swan Mountains, Montana).

ity points was not observed during any season because, by definition, these points had minimal behavioral impact on bears.

Extrapolation of TSA coefficients to the EA revealed that realized habitat effectiveness increased on a northwest-to-southeast gradient due to lower levels of human development, such as trails and relatively permanent camping sites, within designated wilderness areas. Conversely, we observed a general decline in habitat potential from northwest to southeast during all seasons, but most noticeably during spring. This was caused by gradients of increasing elevation and decreasing greenness.

The decline in greenness was related to the topographic position of the Mission Mountains, which created a rain shadow effect within portions of the Bob Marshall Wilderness. Decreased precipitation in the Bob Marshall Wilderness resulted in more contiguous dry forest cover, especially at lower elevations. Although closed-canopy timber was often used by grizzly bears, vegetal foods sought by grizzly bears were generally less abundant in the dry forest types of the Bob Marshall Wilderness than elsewhere (Craighead et al. 1982; Servheen 1983; Mace 1986; Aune & Kasworm 1989). Further, much of the documented grizzly bear use of closed timber habitats in the NCDE was adjacent to open canopy sites with abundant succulent vegetation, such as avalanche chutes, meadows, rock lands, or timber harvest units (Aune & Kasworm 1989; Mace & Waller 1997).

Additionally, during spring telemetry flights we observed that the southern portions of the EA retained winter snow longer than more northerly areas, thus decreasing habitat availability. The lower habitat potential in the Bob Marshall Wilderness during spring corroborates our knowledge of bear density and home-range size. Bear densities were higher and home-ranges smaller in the TSA than in the higher-elevation and drier habitats to the east of the Continental Divide (Aune & Kasworm 1989; Eberhardt & Knight 1996; Mace & Waller 1998).

The Swan Valley exhibited high spring habitat potential for female grizzly bears. This valley, between the

Bob Marshall and Mission Mountain wilderness areas, has been proposed as a linkage zone between these two areas (Sandstrom & Servheen, in press). Grizzly bear observations and conflicts were rare in this valley, suggesting a relatively low density of bears (Mace & Waller 1998). The high road densities and numerous human activity centers in the Swan Valley, which were avoided by female grizzly bears in the TSA, may be precluding grizzly bear movement across the Swan Valley. Obtaining full grizzly bear occupancy in the western portion of the NCDE will require management attention to these and other low-elevation spring habitats. Achieving conservation for bears in this mixture of state, federal, private, and corporate lands will be a continuing challenge.

The greenness band derived from tasseled-cap transformation of TM satellite imagery was a powerful indicator of habitat. Strong selection for greenness by marked grizzly bears was observed during all seasons. Examples of open-canopied vegetation types with high greenness values were avalanche chutes, shrub lands, cutting units, and riparian zones with high canopy coverage of deciduous shrubs such as Alder (*Alnus* spp.) and fool's huckleberry (*Menziesia ferruginea*) (Waller & Mace 1998). Vegetal foods found in such types and eaten by grizzly bears in the Swan Mountains included cow parsnip (*Heracleum lanatum*) and horsetail (*Equisetum* spp.) (Mace & Jonkel 1983). There was no clear connection between greenness, vegetation species composition, and physiography. Similar greenness values can be obtained for vastly different physiographic features (for example, cutting units and avalanche chutes). In fact, the high greenness values in the TSA were due in part to past timber harvest activities that removed overstory conifers. In the TSA some timber harvest units did provide important seasonal foraging areas (Waller 1992; Waller & Mace 1998). Timber harvest units may not be valuable to bears in all areas (Anderson 1994).

We do not suggest that our use of a pseudo-habitat map would be superior to a well-constructed and validated cover-type map. Craighead et al. (1982) suggest that conversion of satellite imagery to a validated map with vegetal and physiographic descriptions should be the ultimate goal of habitat managers in the NCDE and elsewhere.

At present, our method does not incorporate risk of mortality. Risk of mortality can be considered indirect (mortality due to displacement, habitat degradation, and diminished reproductive potential) or direct (immediate death or removal). Areas of high degradation may be interpreted as areas where grizzly bears have a high risk of indirect mortality, but where risk of direct mortality may or may not be high. Conversely, small areas of high potential or effectiveness surrounded by human activity centers may also be areas where risk of direct mortality is great.

Other authors have presented similar concepts based on different methods, including Mahalanobis distance (Clark et al. 1993), discriminant function analysis (Capen et al. 1986), Bayesian probability (Aspinall & Veitch 1993), proximity analysis (Breininger et al. 1991), and logistic regression (Pereira & Itami 1991). Our method has some advantages over previous methods. Model outputs are easily interpreted in terms of relative probability of use, not an arbitrary score. Statistically, the process of logistic regression is well understood, although its application to GIS data is new. Use of RSF values derived from logistic regression appears superior to the "delphi method" currently in place to assign response coefficients. We recommend that habitat managers of other ecosystems that have telemetry information from grizzly bears consider using our methods to derive CEM coefficients and map the relative probability of use on a seasonal basis so that comparisons between ecosystems can be made. Standardized statistical, mapping, and RSF scaling methods would greatly aid in comparisons among ecosystems. Further research linking model coefficients and field data are needed.

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